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Three new non-lacustrine species of the endemic freshwater gastropod genus *Sulawesidrobia* (Caenogastropoda, Truncatelloidea, Tateidae) from Sulawesi, Indonesia, with additional records of species from ancient Lake Poso

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Abstract

The vast majority of freshwater gastropods of the family Tateidae dwell in springs, small streams and the groundwater. In Sulawesi, however, all 31 described species occur in lake habitats. This exclusivity is certainly an artefact, a consequence of the lack of research in non-lacustrine habitats. Indeed, recent explorations discovered three species in non-lacustrine habitats, *Sulawesidrobia lasoloensis* **sp. nov.** and *S. marmer* **sp. nov.** in small streams in Southeast Sulawesi, and *S. tilangaensis* **sp. nov.** in the spring-fed Tilanga natural pool in South Sulawesi. We describe these species based on shell morphology, anatomy as well as mitochondrial sequence data and, based on the latter, inferred their phylogenetic relationships. These analyses also included new samples from Lake Poso. *Sulawesidrobia lasoloensis* **sp. nov.** and *S. marmer* **sp. nov.** formed a sister group to a clade from the Malili-Lake system, whereas *S. tilangaensis* **sp. nov.** was nested among the species from Lake Poso. Considering the long branches as well as the geographic distances between the new species and their respective lake relatives as well as the large unexplored areas, many more species dwelling in similar, for tateids more typical habitats are to be expected.

Key Words

Anatomy, molecular diagnosis, morphology, riverine

Introduction

The exploration and investigation of Sulawesi's freshwater fauna has, with the exception of fish, largely focused on the ancient lakes Lake Poso in the northern central highlands and the lakes of the Malili system – interconnected Lakes Matano, Mahalona, and Towuti as well as the smaller satellite lakes Lontoa, and Masapi – about 75 km further SE. Due to their geology, geological history, and age (Vaillant et al. 2011), these lakes provide a high diversity of habitats which support species-rich radiations that have received substantial recognition by evolutionary biologists. These radiations include, e.g., fish (Parenti and Soeroto 2004; Herder et al. 2006; Stelbrink et al. 2014), crayfish and crabs (von Rintelen et al. 2007; Poettinger and Schubart 2014), and mollusks (von Rintelen and Glaubrecht 2005; von Rintelen et al. 2012; Albrecht et al. 2020; Clewing et al. 2020). Tateid gastropods of the genera *Sulawesidrobia* Ponder & Haase, 2005 and *Keindahan* Haase & Bouchet, 2006 with 29 and two species, respectively, have exclusively been described from lakes (Abbott 1945; Bouchet 1995; Ponder and Haase 2005; Haase and Bouchet 2006; Zielske et al. 2011; Haase et al. 2023). Usually, Tateidae, a family

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of small-sized species distributed from Sulawesi across Australasia, a number of islands and archipelagos in the South Pacific and represented by one genus in South America, inhabit springs, small streams, and the groundwater (Zielske et al. 2017; Ponder 2019). In addition, with *Potamopyrgus antipodarum*, native to New Zealand, the family includes a habitat-generalist, which has very successfully invaded Europe, Australia, North America, Japan, Chile, and lately also the Middle East and North Africa (summarized in Schächinger et al. 2025). Lake-dwelling species, let alone entire, largely endemic lake radiations, are exceptional. However, the exclusivity of the lake habitats of the species from Sulawesi is certainly an artefact, a consequence of the lack of research in non-lacustrine habitats. Also, the much larger species of *Tylomelania* Sarasin & Sarasin, 1897, which belong to the caenogastropod family Pachychilidae and are represented in the ancient lakes by speciose flocks, had an origin in rivers and colonized the lakes several times independently (von Rintelen et al. 2014). Therefore, also for *Sulawesidrobia* a fluviatile origin is plausible. In 2010 and 2023, two expeditions did indeed survey habitats other than lakes – streams in Southeast Sulawesi and the spring-fed Tilanga Natural Pool in South Sulawesi – and brought to light three new species as well as several new samples of known species from Lake Poso. The aim of this paper is to formally describe these new species and analyze the phylogenetic relationships of all new samples based on sequence fragments of two mitochondrial genes.

Material and methods

Collecting

Snails were collected on two occasions. In 2010, Jean-Michel Bichain (Natural History and Ethnography Society Colmar, France) surveyed streams in Southeast Sulawesi. Thirteen years later, Thomas von Rintelen, Muhammad Iqram, and Sara Nejad (all Museum für Naturkunde, Berlin, Germany) collected in Lake Poso, in Southeast Sulawesi, and in the Tilanga natural pool during a field campaign in September and October 2023. For more details of the locality data see Table 1. A map is provided in Fig. 1. The snails were handpicked from rocks, plants, or wood they clung to and preserved in 96% ethanol. In our lab in Greifswald, they were stored at 4 °C. In preparation for further analyses, the specimens were presorted by eye into morphospecies based on the shell morphology under a Zeiss SteReo Discovery V20 microscope.

Vouchering

All samples have been deposited in the malacological collections of Museum Zoologi Bogor (MZB), Museum für Naturkunde Berlin (ZMB), and Musée et Société d'Histoire naturelle et d'Ethnographie de Colmar (MHNEC) as specified in the *Material examined* section for each species and in Table 1.

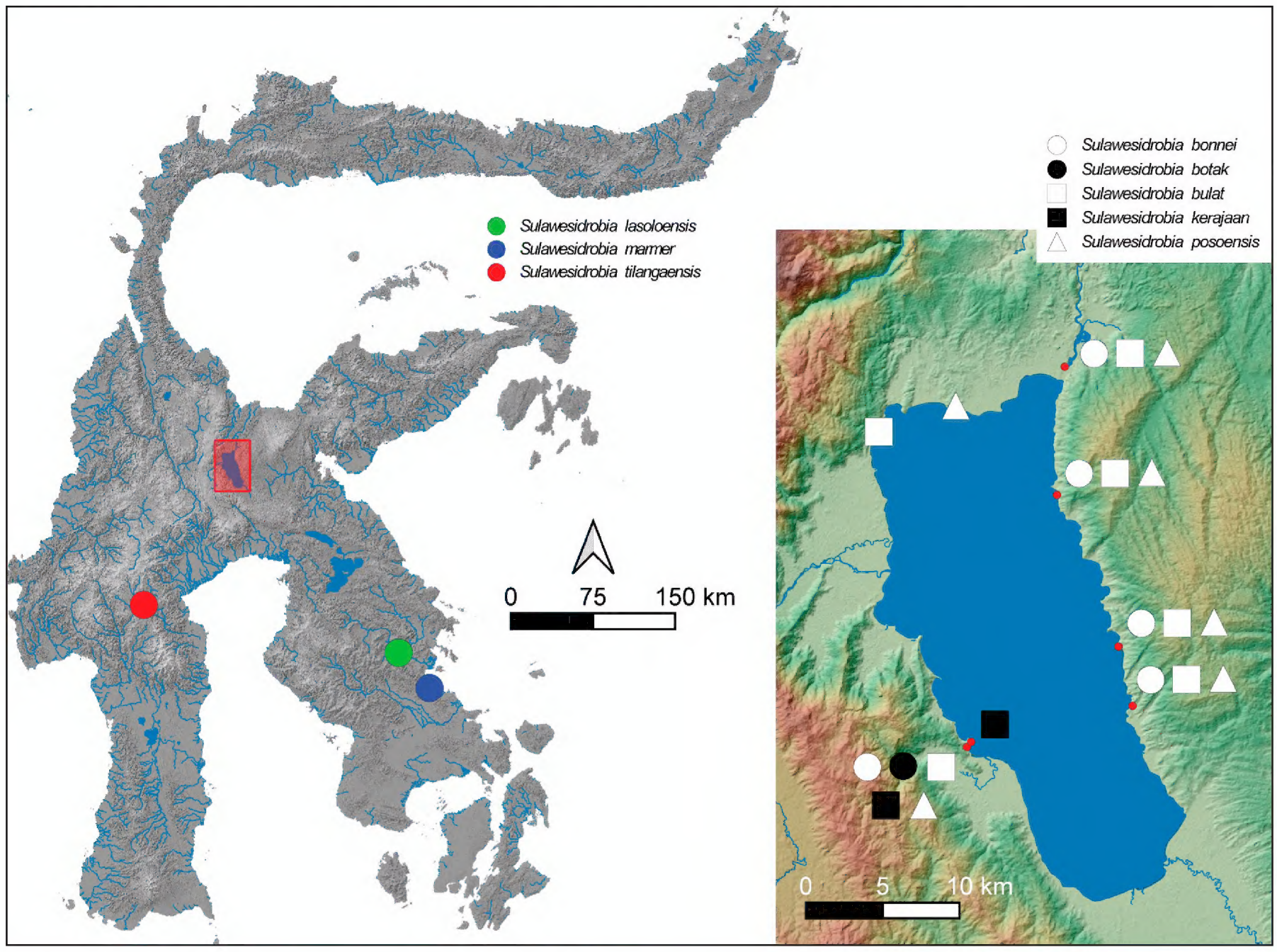

Figure 1. Map showing sampling localities. Inset and to the right: Lake Poso.

Table 1. Locality details including museum catalog and GenBank accession numbers of the new and newly sequenced species. All samples were collected by Thomas von Rintelen, Muhammad Iqram, and Sara Nejad except for *S. lasoloensis* sp. nov. and *S. tilangaensis* sp. nov., which were collected by Jean-Michel Bichain and Muhammad Iqram, respectively.

Species	Museum catalog #	Locality	Coordinates	Date of collection	GenBank # COI	GenBank # 16S
S. lasoloensis sp. nov.	MZB Gst. 12194 ZMB 118374	Tenggara, Amorome, tributary of the Lasolo River	3°25'35.6"S, 121°58'58.4"E	17 July 2010	PV466741	—
S. lasoloensis sp. nov.	MZB Gst. 12195 ZMB 118375	Tenggara, Amorome, tributary of the Lasolo River	3°25'43.1"S, 121°58'57.2"E	17 July 2010	PV466742	—
S. marmer sp. nov.	MZB Gst. 12188 ZMB 118347	Stream on road Wawotobi - Lasolo, S of Abola; on rocks	3°43'06.6"S, 122°14'07.1"E	17 Sept 2023	PV466711–PV466712	—
S. tilangaensis sp. nov.	MZB Gst. 12190 ZMB 118373	Tilanga Natural Pool, Toraja Utara; on karstic rocks	3°02'05.6"S, 119°53'14.3"E	18 Oct 2023	PV466739–PV466740	—
S. bonnei	ZMB 118329	Lake Poso, E shore, S of Tando Bone; on leaves	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466687–PV466688	PV460864
S. bonnei	ZMB 118332	Lake Poso, E shore, S of Tando Bone; on wood	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466692–PV466693	PV460868–PV460869
S. bonnei	ZMB 118334	Poso River, Tentena, N of outflow from Lake Poso; on leaves	1°45'47.5"S, 120°38'22.2"E	21 Sept 2023	PV466696–PV466697	PV460872–PV460873
S. bonnei	ZMB 118339	Lake Poso, W shore, Bay N of Bancea village; on rocks	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466701–PV466702	PV460877 PV460878
S. bonnei	ZMB 118348	Lake Poso, E shore, at Bolo, S of Dulumai; on plants	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466713–PV466714	PV460886 PV460887
S. bonnei	ZMB 118351	Lake Poso, E shore, at Bolo, S of Dulumai; on plants	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466718–PV466719	PV460890 PV460891
S. bonnei	ZMB 118353	Lake Poso, E shore, at Bolo, S of Dulumai; on plants	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466736	—
S. bonnei	ZMB 118356	Lake Poso, E shore, at Bolo, S of Dulumai; on plants	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466723	—
S. bonnei	ZMB 118359	Lake Poso, E shore, at Bolo, S of Dulumai; on leaves	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466725–PV466726	—
S. bonnei	ZMB 118361	Lake Poso, E shore, at Tolambo; on wood	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466728–PV466729	—
S. bonnei	ZMB 118363	Lake Poso, E shore, at Tolambo; on leaves	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466730–PV466732	—
S. botak	ZMB 118340	Lake Poso, W shore, Bay N of Bancea village; on leaves	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466703	PV460879
S. bulat	ZMB 118327	Lake Poso, E shore, S of Tando Bone; on rocks	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466682–PV466684	PV460859–PV460861
S. bulat	ZMB 118333	Lake Poso, W shore, N of Siuri, on rocks	1°48'04.3"S, 120°31'50.9"E	21 Sept 2023	PV466694–PV466695	PV460870–PV460871
S. bulat	ZMB 118335	Poso River, Tentena, N of outflow from Lake Poso; on rocks	1°45'47.5"S, 120°38'22.2"E	21 Sept 2023	PV466698	PV460874
S. bulat	ZMB 118341	Lake Poso, W shore, Bay N of Bancea village; on rocks	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466704–PV466705	PV460880–PV460881
S. bulat	MZB Gst. 12192 ZMB 118349	Lake Poso, E shore, at Tolambo; on rocks	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466715–PV466716	PV460888 PV460889
S. bulat	ZMB 118354	Lake Poso, E shore, at Bolo, S of Dulumai; on wood	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466737	—
S. bulat	ZMB 118357	Lake Poso, E shore, at Bolo, S of Dulumai; on rocks	1°55'37.0"S, 120°40'15.5	20 Sept 2023	PV466724	—
S. bulat	ZMB 118365	Lake Poso, E shore, at Tolambo; on leaves	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466734	—
S. bulat	ZMB 118367	Lake Poso, E shore, at Tolambo; on leaves	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466735	—
S. kerajaan	ZMB 118160	Lake Poso, W shore, Cape Bancea	1°58'56.6"S, 120°35'04.6"E	4 Aug 2018	PV466743–PV466745	—
S. kerajaan	ZMB 118338	Lake Poso, W shore, Bay N of Bancea village; on leaves	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466700	PV460876
S. kerajaan	ZMB 118344	Lake Poso, W shore, Bay N of Bancea village; on wood	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466708	PV460883
S. posoensis	ZMB 118326	Poso River, Tentena, N of outflow from Lake Poso; on wood	1°45'47.5"S, 120°38'22.2"E	21 Sept 2023	PV466680–PV466681	PV460858
S. posoensis	ZMB 118328	Lake Poso, E shore, S of Tando Bone; on leaves	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466685–PV466686	PV460862–PV460863
S. posoensis	ZMB 118330	Lake Poso, E shore, S of Tando Bone; on wood	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466689–PV466690	PV460865–PV460866
S. posoensis	ZMB 118331	Lake Poso, E shore, S of Tando Bone; on wood	1°50'17.5"S, 120°38'06.0"E	21 Sept 2023	PV466691	PV460867
S. posoensis	ZMB 118336	Poso River, Tentena, N of outflow from Lake Poso; on rocks	1°45'47.5"S, 120°38'22.2"E	21 Sept 2023	PV466699	PV460875
S. posoensis	ZMB 118342	Lake Poso, W shore, Bay N of Bancea village; on rocks	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466706–PV466707	PV460882

Species	Museum catalog #	Locality	Coordinates	Date of collection	GenBank # COI	GenBank # 16S
S. posoensis	ZMB 118345	Lake Poso, W shore, Bay N of Bancea village; on wood	1°59'04.2"S, 120°34'58.8"E	21 Sept 2023	PV466709–PV466710	PV460884 PV460885
S. posoensis	ZMB 118350	Lake Poso, E shore, at Tolambo; on rocks	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466717	—
S. posoensis	ZMB 118352	Lake Poso, E shore, at Bolo, S of Dulumai; on wood	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466720	—
S. posoensis	ZMB 118355	Lake Poso, E shore, at Bolo, S of Dulumai; on rocks	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466721–PV466722	PV460892 PV460893
S. posoensis	ZMB 118360	Lake Poso, E shore, at Bolo, S of Dulumai; on leaves	1°55'37.0"S, 120°40'15.5"E	20 Sept 2023	PV466727	—
S. posoensis	ZMB 118362	Lake Poso, E shore, at Tolambo; on wood	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466738	—
S. posoensis	ZMB 118364	Lake Poso, E shore, at Tolambo; on leaves	1°57'41.4"S, 120°40'44.8"E	20 Sept 2023	PV466733	—

Morphology and anatomy of the new species

To ensure comparability, up to 20 adult snails distinguishable by their continuous apertural lips were selected for morphometry. They were placed in a silicone-coated small Petri dish with their apertures facing upwards and maximizing the projections in x and y directions under a Zeiss SteReo Discovery V20 microscope equipped with an Axiocam 305 Color camera. All images were taken at the same magnification and five dimensions (shell height, SH; shell width, SW; aperture height, AH; aperture width, AW; width of the bodywhorl, BWW) were measured parallel or perpendicular to the coiling axis using the Zeiss Axio Vision program (version 4.8.2). Whorls were counted to the closest eighth of a whorl as described by Verduin (1982).

A repeatability test was conducted in order to control the consistency of shell orientation and measurements. Twenty snails were photographed and measured on the same day by LK as described above. This process was repeated after 14 days with the same individuals. Normal distribution of the data was examined visually by histograms and by the Shapiro-Wilk normality test. The normally distributed SH, SW, and BWW data was then analyzed with a paired t-test and the non-parametric AH and AW data was compared with the Wilcoxon signed rank test using PAST version 4.03 (Hammer et al. 2001) and RStudio version 2023.09.1 (R Core Team 2022/23, respectively. There were no significant differences between the two measurement series ($p > 0.05$ for all dimensions).

In order to visualize the morphological variation and discriminate the new species, we conducted a principal component analysis (PCA) based on a correlation matrix of the six dimensions and a discriminant analysis followed by a MANOVA, respectively, in PAST. Mardia tests and Doornik and Hansen's omnibus test did not reject multivariate normality ($p > 0.05$).

For anatomical investigations, shells of selected specimens were dissolved in 1N HCl. Snails were dissected with minute pins in water under a Nikon SMZ 800 stereo microscope equipped with a DS-2Mv camera. Drawings were made from photographs. For scanning electron microscopy (SEM) in a Zeiss EVO LS10 SEM, shells and radulae were cleaned in c. 5% sodium hypochlorite. Heads and penes were dried in hexamethyldisilazane (Nation 1983). Coating was conducted with palladium/platinum with a Fisons Polaron SC7640 sputter coater.

DNA extraction and sequencing

DNA was extracted from one or two subadult snails per morphospecies using the E.Z.N.A.® Mollusc DNA Kit (Omega Bio-tek) according to the manufacturer's protocol. The NanoDrop™ ND 1000 Spectrophotometer (Peqlab) and a 1% agarose gel were used to quantify and assess the purity of the extracted DNA. Two mitochondrial fragments, cytochrome c oxidase subunit I (COI) and 16S rRNA (16S) were sequenced. Polymerase chain reactions (PCR) were conducted in a mix containing 2.5 µl 10×NH4 Buffer (Bioline), 2.0 µl $MgCl_2$ (50 mM stock), 0.5 µl dNTP (10 mM stock), 0.1 µl MyTaq™ Mix (Bioline), 16.0 µl H_2O, 1.0 µl BSA (1% stock), along with 1 µl each of both forward and backward primers (10 pmol stock) as well as 1.0 µl of the extracted DNA. The primers used for amplifying COI were LCO1490 of Folmer et al. (1994) and HCOmod of Zielske et al. (2011). 16S was amplified with 16Sar and 16br described by Palumbi et al. (1991). The PCR temperature profile for COI was 3 min of initial denaturation at 95 °C, 40 cycles of denaturation at 95 °C for 45 s, annealing at 46 °C for 45 s, and extension at 72 °C for 90 s, and a final extension at 72 °C for 7 min. For 16S, a touchdown protocol was run with 1 min of initial denaturation at 95 °C followed by 10 cycles encompassing denaturation at 95 °C for 20 s, annealing dropping from 60 to 51 °C in each cycle for 20 s, and extension at 72 °C for 30 s, then 25 cycles with 95 °C for 20 s, 51 °C for 20 s, and 72 °C for 30 s, and the final extension at 72 °C for 5 min. The amplification products were visualized by gel electrophoresis and purified with 1.5 µl Exonuclease I (BioLabs) and Shrimp Alkaline Phosphatase (BioLabs). The DNA concentration was measured with the NanoDrop™ and diluted to approximately 40 ng/µl. Cycle-sequencing was performed in a 10 µl reaction volume using 4.85 µl H_2O, 1.0 µl SupreDye cycle-sequencing mixture (ADS), 1.0 µl 5× Sequencing Buffer (ADS), 0.15 µl of the respective primer, and 3 µl amplification product. The cycle-sequencing conditions were 1 min. of initial denaturation at 96 °C followed by 25 cycles comprising 96 °C for 10 s, 46 °C (COI) or 48 °C (16S) for 5 s, and 60 °C for 4 min. The products were purified using the Agencourt CleanSEQ magnetic bead kit (Beckman Coulter) and sequenced with a 3130xl Genetic Analyzer (Thermo Fisher Scientific).

Phylogenetic analysis

Sequences were edited in Geneious version 10.2.6 (Kearse et al. 2012). They were complemented with almost all sequences published by Haase et al. (2023) including the outgroup species *Edgbastonia alanwillsi* Ponder, 2008, *Jardinella tumorosa* Ponder, 1991, and *Trochidrobia punicea* Ponder, Hershler and Jenkins, 1989. Only a few specimens of *S. anceps* Zielske, Glaubrecht & Haase, 2011, *S. datar* Zielske, Glaubrecht & Haase, 2011, and *S. megalodon* Zielske, Glaubrecht & Haase, 2011 were omitted. Note that GenBank numbers for *S. botak* Haase & Bouchet, 2006, and *S. kerajaan* Haase & Bouchet, 2006, were swapped by Zielske et al. (2011), still wrong in Haase et al. (2023), but now corrected. GenBank accession numbers of newly sequenced specimens are given in Table 1. MEGA-X version 10.2.6 (Kumar et al. 2018) was used to align the COI sequences with ClustalW (Thompson et al. 1994) and the 16S sequences with MUSCLE (default settings; Edgar 2004). The aligned sequences were then concatenated to a total length of 1175 bp in the same program. The best-fitting nucleotide substitution models for each gene were inferred in jModeltest version 2.1.4 (Darriba et al. 2012) based on the Bayesian information criterion. The model recommended was HKY + G + I for either gene. Maximum Likelihood (ML) and Bayesian Inference (BI) were used to infer the phylogenetic relationships. The ML tree was reconstructed with 1000 fast-bootstrap replicates using IQ-TREE (Trifinopoulos et al. 2016). BI analyses were conducted in MrBayes version 3.2.7 (Ronquist et al. 2012) with the number of generations set to 3.000.000 saving every 100th tree, a burnin of 7500, and otherwise default settings. Convergence of parameter estimates was assessed using the diagnostics implemented in MrBayes. Both trees were drawn and edited in FigTree version 1.4.4 (https://github.com/rambaut/figtree/releases).

Molecular diagnosis

For one of the new species only five adult specimens were available, which we did not want to destroy for anatomical investigations. For this species we extracted molecular diagnostic characters of type 1 (fixed base different from other taxa) from the COI alignment (Suppl. material 1) using the R (version 4.2.0; R Core Team 2022/2023) package QUIDDICH (Kühn and Haase 2020).

Results

Systematic descriptions

Measurements of the new species are given in Table 2 and are therefore not included in detail in the species descriptions.

Table 2. Shell measurements and summary statistics. SH, shell height; SW, shell width; AH, aperture height; AW, aperture width; BWW, body whorl width, W, number of whorls; SD, standard deviation; CV, coefficient of variation corrected for unequal sample sizes. Measurements in mm.

Species		SH	SW	AH	AW	BWW	SH/ SW	W
S. lasoloensis sp. nov.	Holotype	1.76	0.94	0.75	0.64	0.84	1.87	3.875
ZMB 118374	min	1.64	0.92	0.75	0.63	0.76	1.71	3.500
N = 20	max	1.98	1.05	0.88	0.75	0.91	2.01	4.125
	mean	1.78	0.98	0.81	0.69	0.83	1.82	3.838
	median	1.77	0.98	0.81	0.69	0.84	1.83	3.875
	SD	0.08	0.04	0.04	0.03	0.04	0.08	0.135
	CV	4.88	4.31	5.00	5.17	5.48	4.58	3.697
S. lasoloensis sp. nov.	min	1.68	1.00	0.77	0.67	0.86	1.55	3.625
ZMB 118375	max	1.91	1.12	0.90	0.73	0.94	1.83	4.125
N = 12	mean	1.80	1.06	0.83	0.70	0.90	1.69	3.938
	median	1.80	1.06	0.82	0.69	0.90	1.68	4.000
	SD	0.07	0.04	0.04	0.02	0.02	0.07	0.146
	CV	4.32	3.70	5.39	2.76	2.83	4.44	3.892
S. marmer sp. nov.	Holotype	1.88	1.15	0.76	0.64	0.99	1.64	4.000
N = 8	min	1.68	1.00	0.76	0.63	0.87	1.55	3.625
	max	2.19	1.29	0.96	0.80	1.15	1.70	4.500
	mean	1.89	1.16	0.82	0.71	1.00	1.63	3.979
	median	1.85	1.15	0.80	0.70	0.10	1.65	4.000
	SD	0.17	0.10	0.06	0.05	9.60	0.06	0.231
	CV	9.55	9.43	8.10	7.87	10.08	3.62	6.104
S. tilangaensis sp. nov.	Holotype	1.77	1.12	0.75	0.68	1.01	1.58	3.500
N = 8	min	1.53	1.07	0.68	0.65	0.96	1.42	3.250
	max	1.95	1.20	0.82	0.76	1.07	1.63	3.750
	mean	1.74	1.12	0.74	0.69	1.01	1.56	3.475
	median	1.74	1.12	0.74	0.68	1.01	1.58	3.500
	SD	0.15	0.05	0.05	0.04	0.04	0.09	0.185
	CV	9.05	4.72	7.33	6.39	4.27	5.78	4.715

Class: Gastropoda Cuvier, 1795
Subclass: Caenogastropoda Cox, 1960
Family: Tateidae Thiele, 1925
Genus: *Sulawesidrobia* Ponder & Haase, 2005

***Sulawesidrobia lasoloensis* sp. nov.**
https://zoobank.org/9640D166-F130-4D55-9F65-956833ACCB80

Etymology. This species is named after the Lasolo River as it is the first description of a *Sulawesidrobia* occurring in the system of this river.

Material examined. ***Holotype*** (Fig. 2A): Indonesia • Sulawesi, North Konawe Regency, Amorome, northeast of Tambua, in a tributary of the Lasolo River. 3°25'35.6"S, 121°58'58.4"E. July 2010; Jean-Michel Bichain leg.; MZB Gst. 12193.

Paratypes (Fig. 3A, B): Indonesia • $N = 20$; same collection data as for holotype; MZB Gst. 12194. $N = 20$; same collection data as for holotype; ZMB 118374. $N = 10$; same collection data as for holotype; MHNEC-MOLL 2025_04_001. $N = 8$; Sulawesi, North Konawe Regency, Amorome, northeast of Tambua, in a tributary of the Lasolo River. 3°25'43.1"S, 121°58'57.2"E. July 2010; Jean-Michel Bichain leg. MZB Gst. 12195. $N = 7$; same collection data, ZMB 118375.

Diagnosis. This new species is characterized by the cylindro-conical shell shape, the anterodorsal insertion of the bursal duct in the ovoid bursa copulatrix, and the penis resting in U-shape with a swelling in the distal third on the left side and a small, round lobe on the right side behind the swelling.

Description. ***Shell.*** Cylindro-conical to conical, slender, 1.7 to 2 times higher than wide, 3.5 to 4.125 whorls, sutures shallow, whorls moderately flat in profile, semitranslucent, goldish-brown, periostracum without color (Figs 2A, 3A, B); protoconch ($N = 4$) wrinkled comprising 0.8–1 whorls (Fig. 4A), teleoconch with growth lines, otherwise without structure; umbilicus a narrow slit; outer lip straight.

Operculum ($N = 9$). Light orange to yellow, thin, paucispiral, nucleus eccentric,

External features ($N = 9$). General appearance fairly light, black pigmentation rather sparse, but variable; eyes black, epidermal black pigment spots almost like eyebrows behind and toward the inner side of the eyes, tentacles otherwise white, proximal region of snout and head pigmented, mirrored, sickle-shaped spots on pharynx; mantle more or less loosely pigmented, almost unpigmented over distal genital glands in both sexes, upper parts of whorls darker than lower ones.

Mantle cavity ($N = 8$). Gill with 10–13 filaments almost abutting to pericard; osphradium ovate to elongate-ovate, about 1/3 of length of gill, rather behind middle of gill.

Digestive system ($N = 3$ for radula, 9 for rectum and stomach). Radula formula R: 4-5 1 4-5/2-3 2-3; L: 3-4 1 4-5, M1: 16-22, M2: 20-25; lateral tooth with membranous junction between face and flank (Fig. 5); stomach without caecum, outer side brown to black; rectum makes a short loop in roof of mantle cavity underneath distal genital glands, more conspicuous in males than in females (Fig. 6A–C).

Female genitalia ($N = 5$; Fig. 7A-C). Ovary a simple sac, starting 1–1.5 whorls below apex, comprising 0.25 to almost 0.5 whorls, reaching stomach; renal oviduct with U-shaped loop followed by 270°-loop underneath ovoid bursa copulatrix lying largely behind albumen gland, bursal duct short emerging anterodorsally, no receptaculum seminis, sperm storage in distal part of second oviduct loop; albumen gland milky-white,

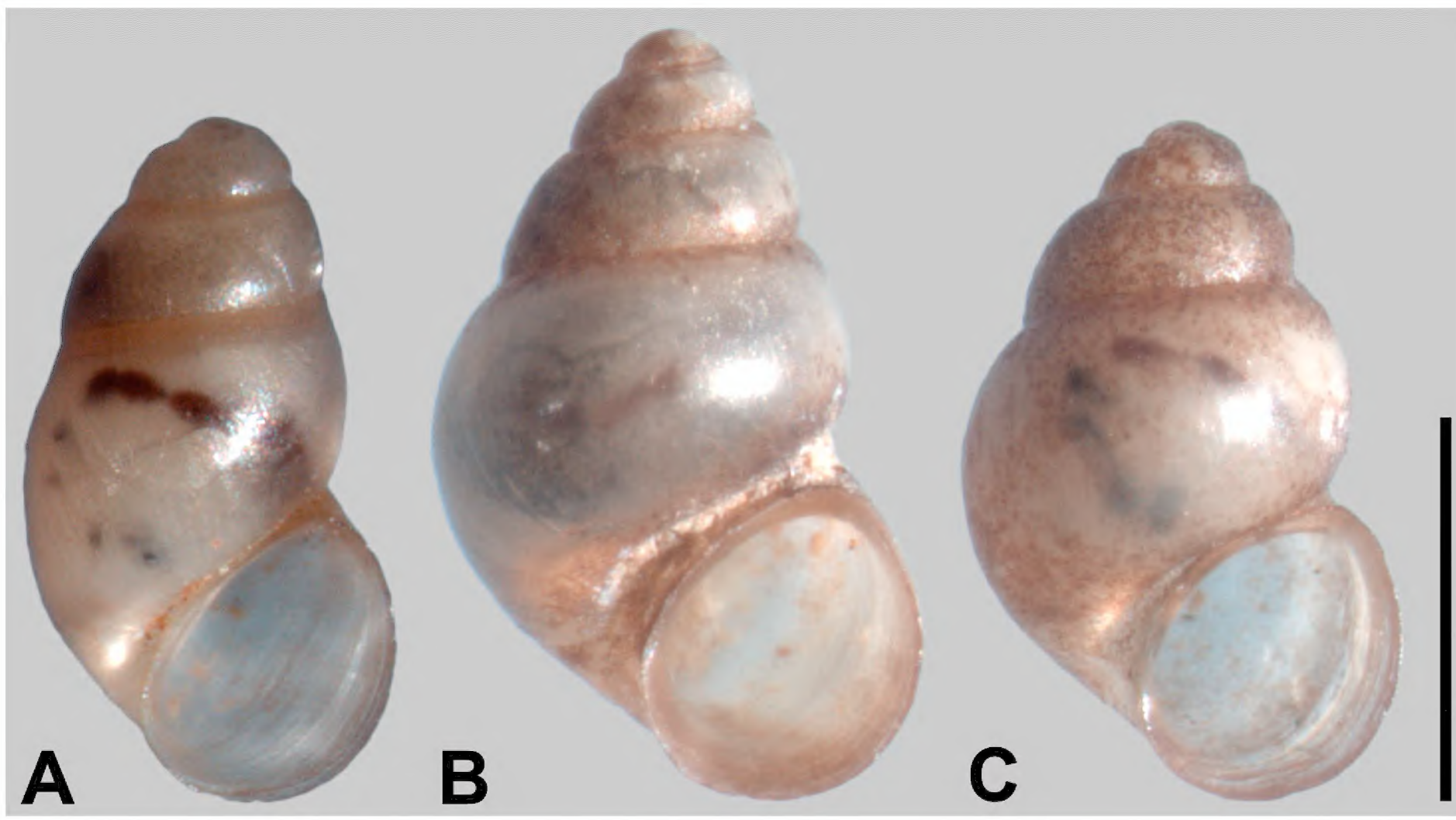

Figure 2. Holotypes. **A.** *S. lasoloensis* sp. nov.(MZB Gst. 12193); **B.** *S. marmer* sp. nov. (MZB Gst. 12187); **C.** *S. tilangaensis* sp. nov. (MZB Gst. 12189). Scale bar: 1 mm.

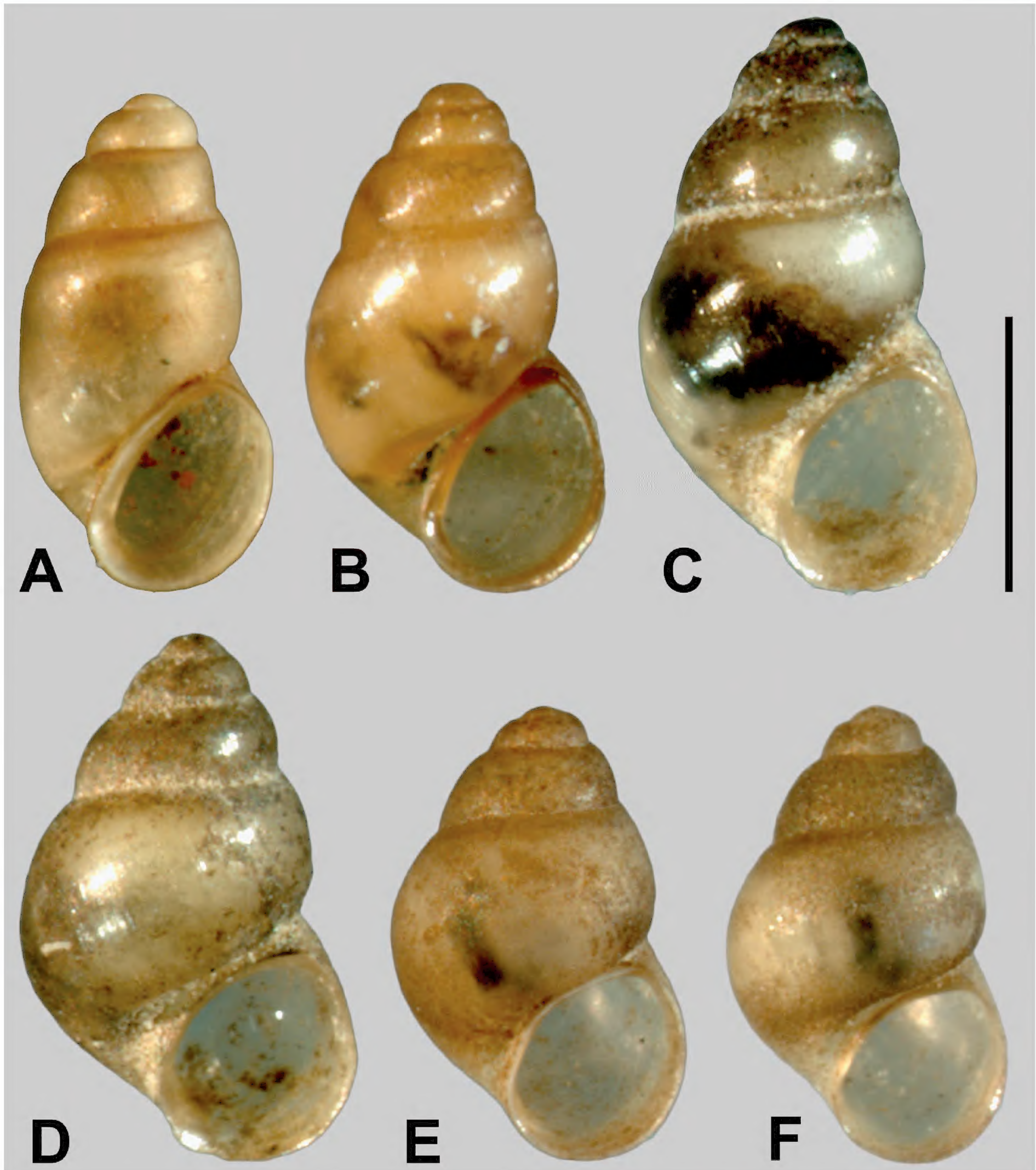

Figure 3. Paratypes. **A, B.** *S. lasoloensis* sp. nov. (ZMB 118374, ZMB 118375); **C, D.** *S. marmer* sp. nov. (ZMB 118347); **E, F.** *S. tilangaensis* sp. nov (ZMB 118373). Scale bar: 1 mm.

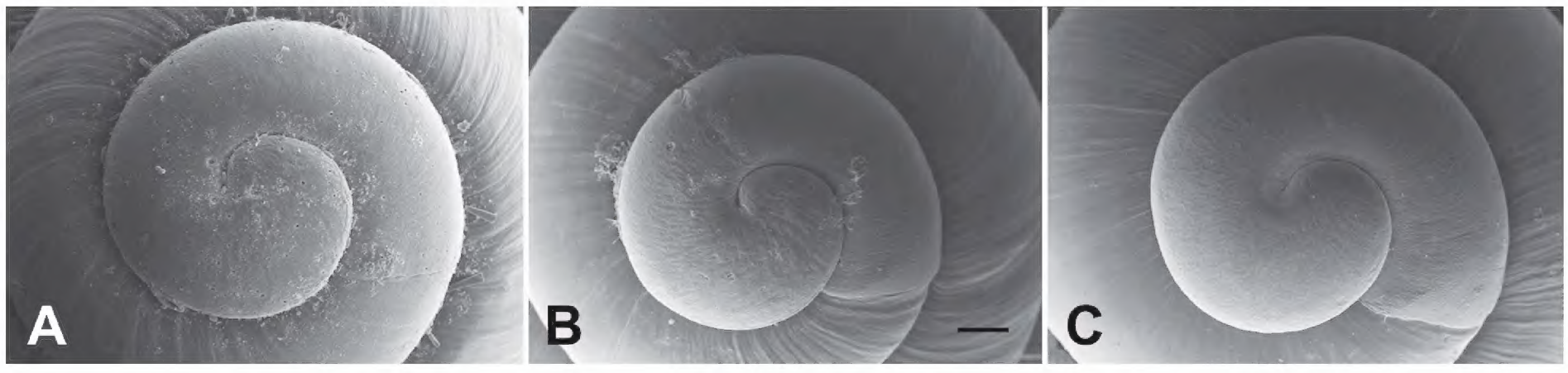

Figure 4. Protoconch. **A.** *S. lasoloensis* sp. nov. (ZMB 118374); **B.** *S. marmer* sp. nov. (ZMB 118347); **C.** *S. tilangaensis* sp. nov. (ZMB 118373). Scale bar: 50 µm.

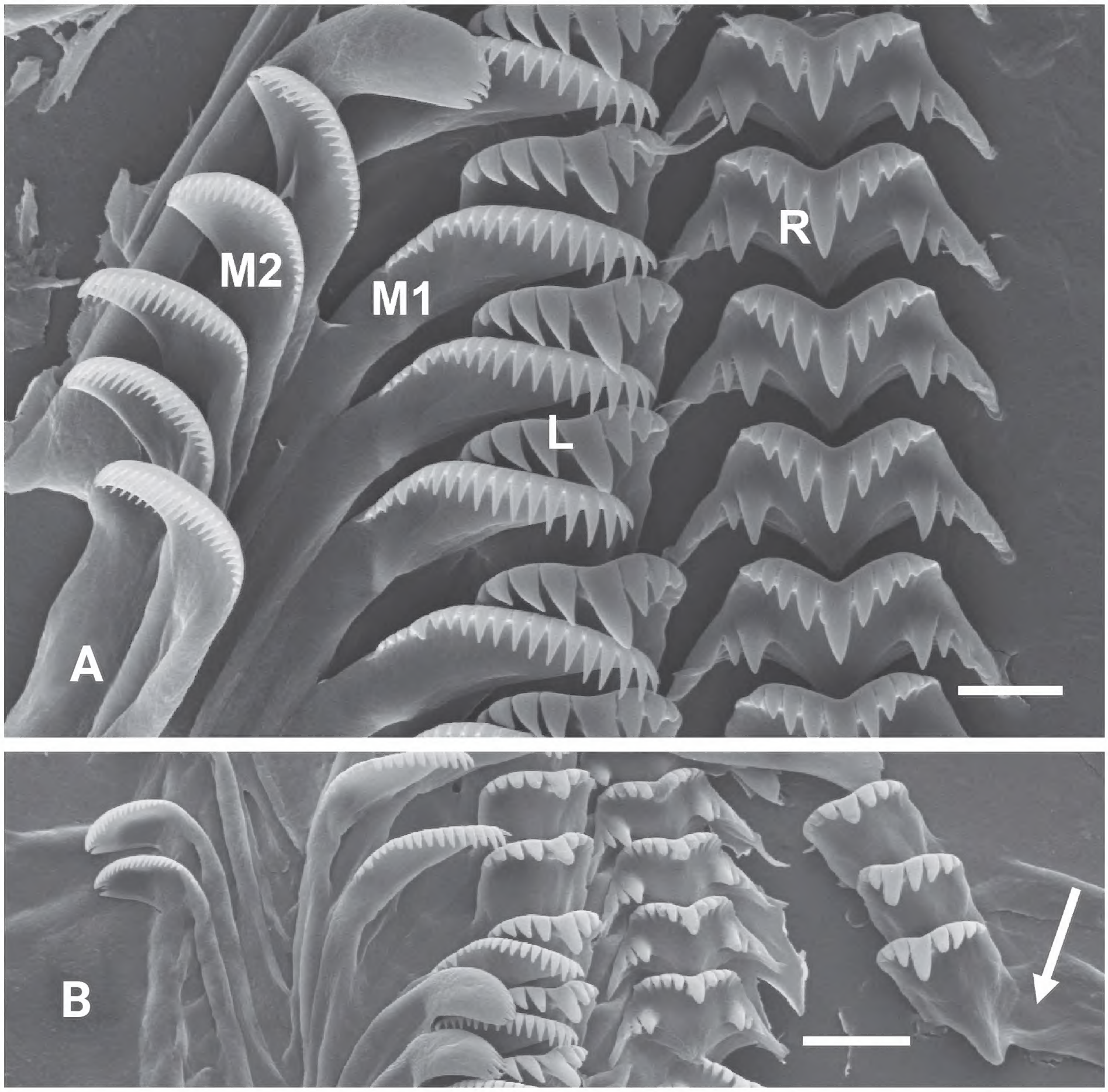

Figure 5. Radula of *S. lasoloensis* sp. nov. **A, B.** From 2 different individuals. Arrow pointing at membranous junction between face and flank of lateral tooth. L, lateral tooth; M1, inner marginal tooth; M2, outer marginal tooth; R, rachis or central tooth. Scale bars: 5 µm (**A**); 10 µm (**B**).

capsule gland bipartite with a posterior opaque white and an anterior milky-white portion.

Male genitalia (N = 4). Testis lobate, starting 0.75 to 1.25 whorls below apex, comprising more than 1 whorl, reaching or overlapping proximal part of stomach; vesicula seminalis coiling underneath distal half of testis; penis in rest U-shaped, tip pointing forward, for most of the length with parallel sides, a swelling in the distal third on the left side and a small, round lobe on the right side behind the swelling (Fig. 8A), penial base with black pigment.

Remarks. The cylindro-conical form of this new species is rare among species of *Sulawesidrobia* and only seen in *S. angusta* Haase & Bouchet, 2006 from Lake Poso (Haase and Bouchet 2006), which has a smaller aperture and less convex whorls, though. The shapes of bursa copulatrix and penis are unique. The morphological variation at the type locality was higher than in the other stream with the slender forms occurring only in the former (Fig. 9). The broader form approaches *S. marmer* sp. nov. described below but differs through the smaller size, the less translucent shell, and the gold-brown color. Both species were well supported as sister species in the phylogenetic analyses. Their relationship to a clade of the Malili Lake system including *S. abreui* Zielske, Glaubrecht & Haase, 2011, received moderate support (Figs 10, 11).

This species is the only species from Sulawesi where a membranous junction between face and flank in the lateral radular teeth typical for the majority of Pacific tateids (e.g., Haase and Zielske 2015) has been observed so far.

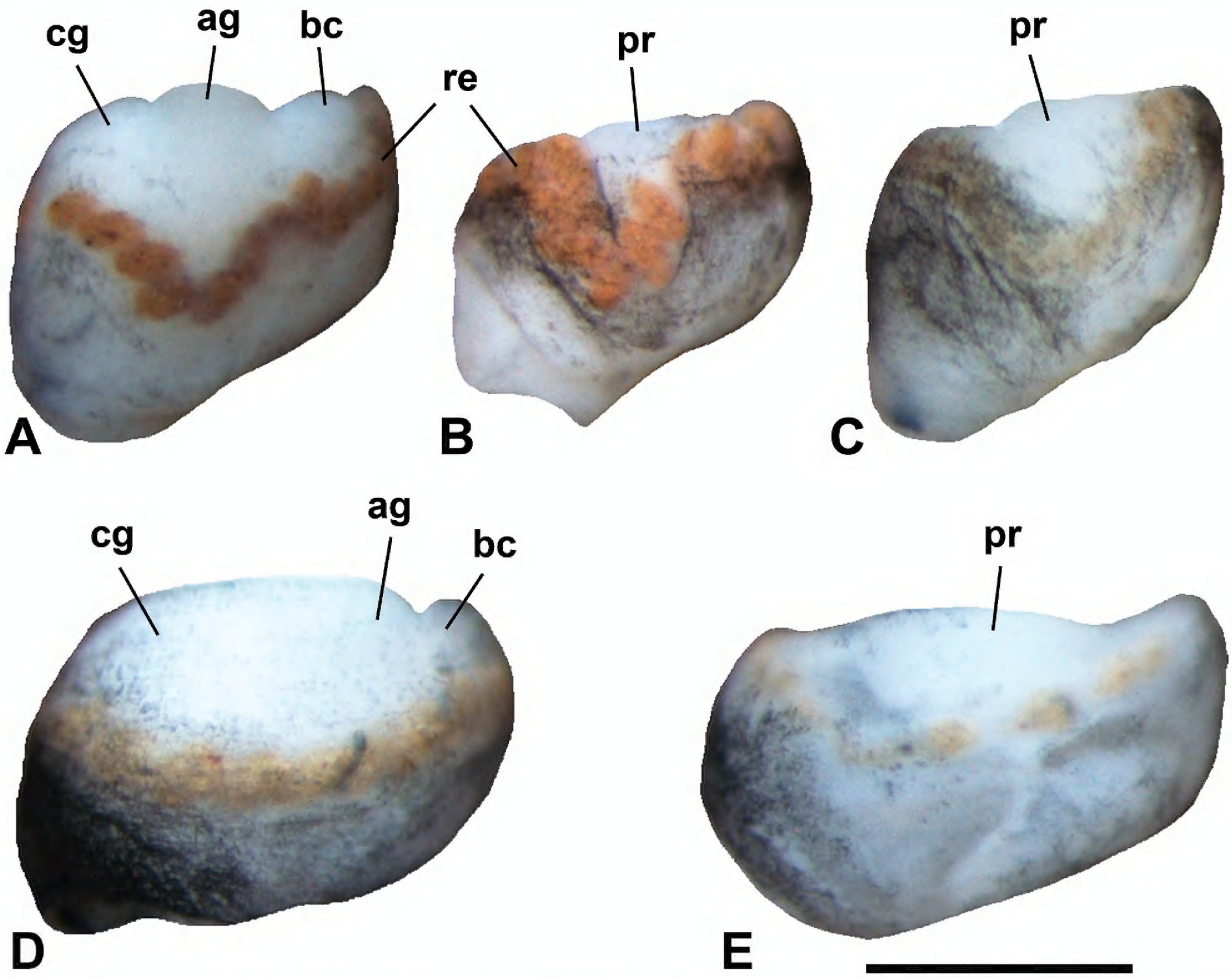

Figure 6. Rectum. **A–C.** *S. lasoloensis* sp. nov.; **D, E.** *S. marmer* sp. nov. **A, D.** Females, **B, C, E.** Males. ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; pr, prostate; re, rectum (filled with fecal pellets). Scale bar: 500 µm.

***Sulawesidrobia marmer* sp. nov.**

https://zoobank.org/8976CBC4-97EF-4A14-9144-5BC707F3A570

Etymology. The word *marmer* is Indonesian and means marble. It refers to the shell's appearance reminiscent of marble and is used as noun in apposition.

Material examined. ***Holotype*** (Fig. 2B): Indonesia • Sulawesi, North Konawe Regency, Lasolo, south of Abola, in a small stream next to the Wawotobi Road, on rocks. 3°43'06.6"S, 122°14'07.1"E. September 2023; Thomas von Rintelen, Muhammad Iqram, and Sara Nejad leg. MZB Gst. 12187.

Paratypes (Fig. 3C, D): Indonesia • $N = 15$; same collection data as for holotype; MZB Gst. 12188. $N = 15$; same collection data as for holotype; ZMB 118347.

DIAGNOSIS. This new species has the conical shell shape and female genitalia seen in several species of *Sulawesidrobia*. But the translucent shell with its light-brown to whitish-grey appearance is characteristic. The coiled penis with the hook-shaped appendage pointing backwards is unique.

Description. ***Shell.*** Conical, 1.6 to 1.7 times higher than wide, 3.625 to 4.5 whorls, sutures shallow, whorls moderately convex, transparent. light-brown to greyish, periostracum without colour (Figs 2B, 3C, D); protoconch ($N = 3$) wrinkled with 0.8 to slightly more than 1 whorls (Fig. 4B), teleoconch with growth lines, otherwise without structure; umbilicus narrow; outer lip straight.

Operculum ($N = 2$). Light orange, thin, paucispiral, nucleus eccentric.

External features ($N = 2$). General appearance fairly dark, black pigmentation particularly dense on snout, behind eyes, anterior parts of mantle and upper parts of whorls; eyes black; tentacles less dark with central white stripe; mirrored, sickle-shaped spots on pharynx; mantle almost unpigmented over distal genital glands in both sexes.

Mantle cavity ($N = 2$). Gill with 17–18 filaments almost abutting to pericard; osphradium elongate, about 2/5 of length of gill, behind middle of gill.

Digestive system ($N = 2$, for radula 1). Radula formula R: 4 1 4/1-2 1-2, L: 3 1 4, M1: 15-18, M2: 20-23; lateral tooth with solid junction between face and flank; stomach without caecum; rectum running along distal genital glands, less closely to prostate than to pallial oviduct.

Female genitalia ($N = 1$; Fig. 7D, E). Ovary a simple sac, starting 1.5 whorls below apex, comprising 0.75 whorls, extending over proximal parts of stomach; renal oviduct undulating before final loop continuing into

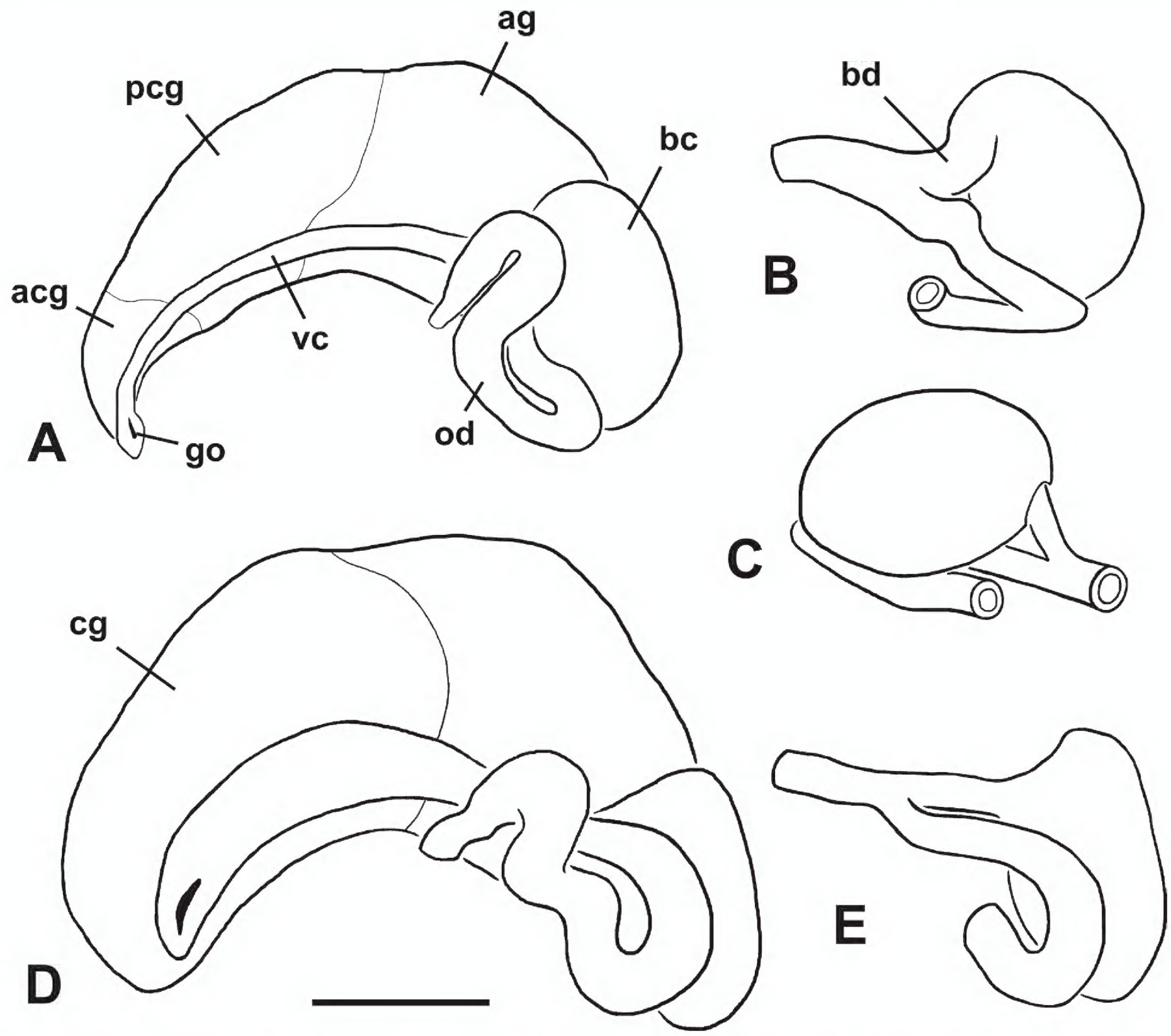

Figure 7. Female genitalia. **A–C.** *S. lasoloensis* sp. nov.; **D, E.** *S. marmer* sp. nov. **A, D.** Situs; **B, C, E.** Bursa copulatrix. acg, anterior capsule gland; ag, albumen gland; bc, bursa copulatrix; bd, bursal duct; cg, capsule gland; go, genital opening; od, oviduct; pcg, posterior capsule gland; vc, ventral channel. Scale bar: 200 µm.

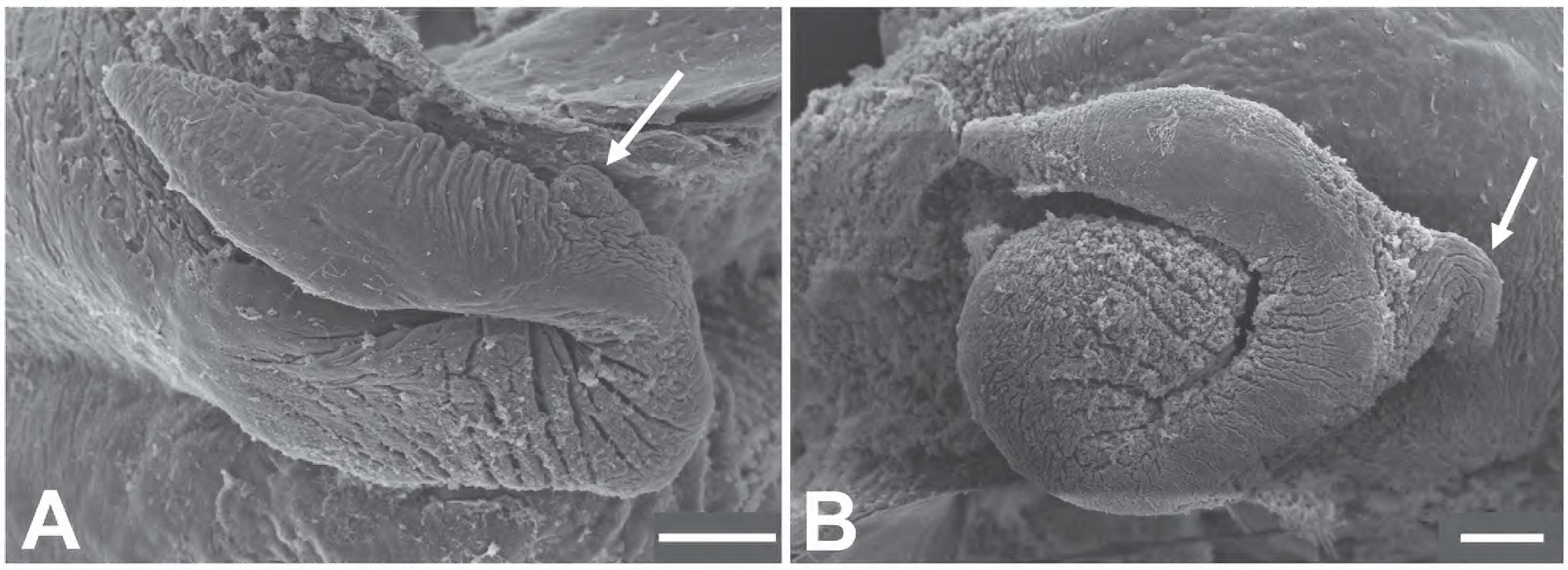

Figure 8. Penis. **A.** *S. lasoloensis* sp. nov; **B.** *S. marmer* sp. nov. Arrows point at lobes. Scale bars: 50 µm.

ventral channel; bursa copulatrix largely behind albumen gland, elongate-ovoid, bursal duct emerging anteroventrally; no receptaculum seminis, sperm storage in distal part of final oviduct loop; albumen gland milky-white, capsule gland opaque white.

Male genitalia ($N = 1$). Testis lobate, starting 1 whorl below apex, comprising about 1 whorl, overlapping proximal part of stomach; vesicula seminalis coiling underneath distal quarter of testis; penis coiling over neck, without pigment, distal part broadened before tapering to

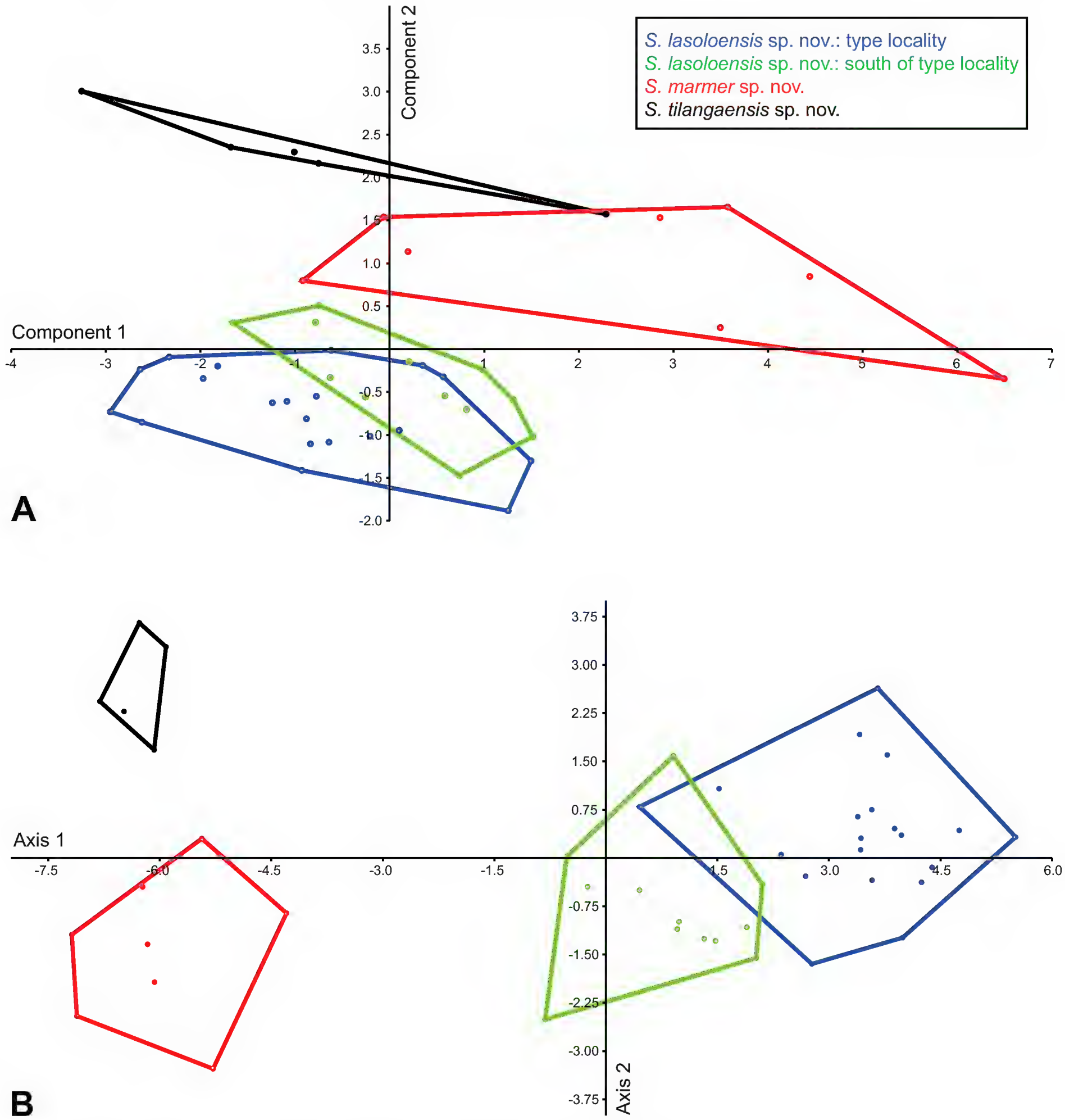

Figure 9. Morphometry. **A.** Principal component analysis; **B.** Discriminant analysis.

pointed tip, small hook pointing backwards on right side just behind broadening (Fig. 8B).

Remarks. The phylogenetic relationships are discussed in the Remarks to *S. lasoloensis* sp. nov. above.

Sulawesidrobia tilangaensis sp. nov.

https://zoobank.org/70AD5707-1058-4EA7-B018-67AE0E6EDC38

Etymology. This species is named after the type locality, the Tilanga natural Pool.

Material examined. ***Holotype*** (Fig. 2C): Indonesia • Sulawesi, Tana Toraja Regency, Makale Utara, Tilanga natural Pool, on karstic rocks. 3°02'05.6"S, 119°53'14.3"E. October 2023, Muhammad Iqram leg. MZB Gst. 12189.

Paratypes (Fig. 3E, F): Indonesia • $N = 4$; same collection data as for holotype; MZB Gst. 12190. $N = 3$; same collection data as for holotype; ZMB 118373.

Diagnosis. This new species is among the smaller and wider conical species of *Sulawesidrobia* morphologically falling into the variation of *S. bonnei*. It is characterized by fixed bases at 18 diagnostic positions in the COI alignment not shared with *S. bonnei*, *S. bulat*, or *S. posoensis*, which are reciprocally paraphyletic (for details see Remarks).

Shell. ($N = 5$). Conical, short, 1.4 to 1.6 times higher than wide, 3.25 to 3.75 whorls, sutures shallow, whorls moderately convex, semitranslucent, light brown, periostracum without color (Figs 2C, 3E, F); protoconch ($N = 1$) wrinkled with slightly more than 1 whorl

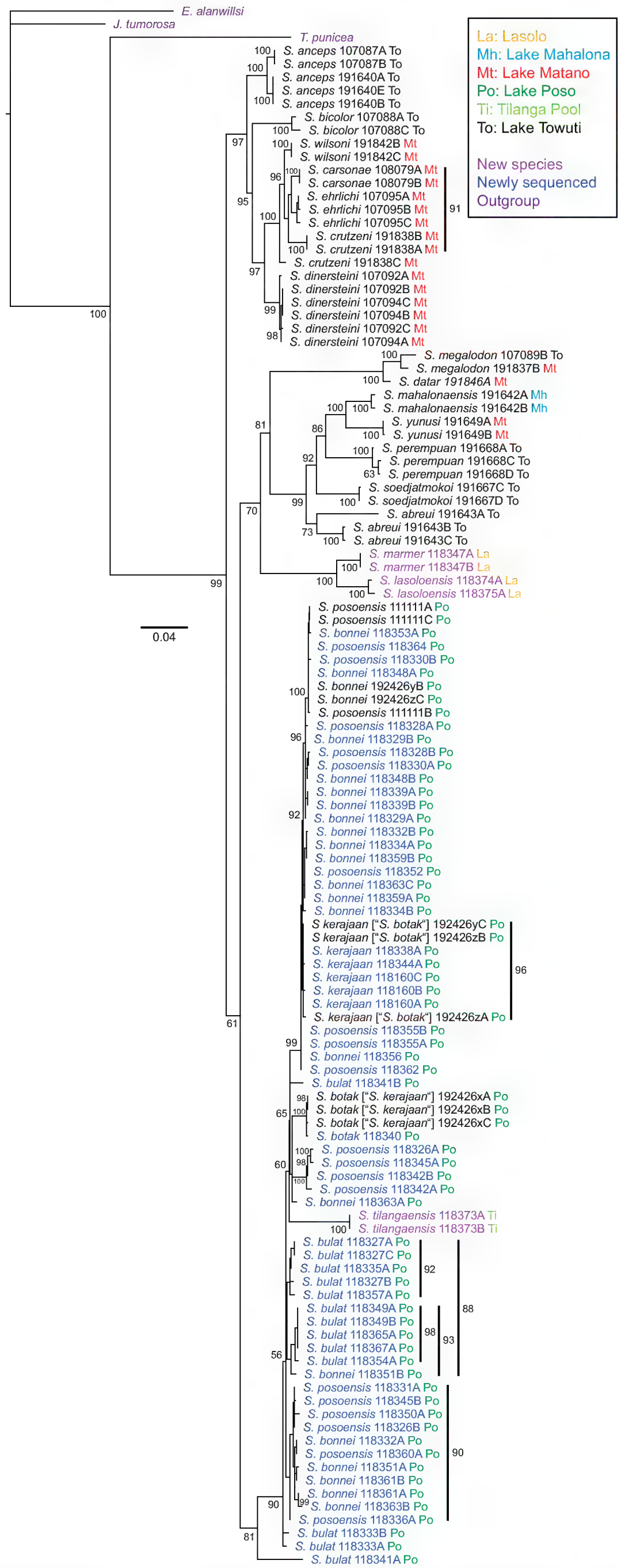

Figure 10. Maximum likelihood tree. Bootstrap values given if > 50 and provided graphical resolution due to short branch lengths permitting.

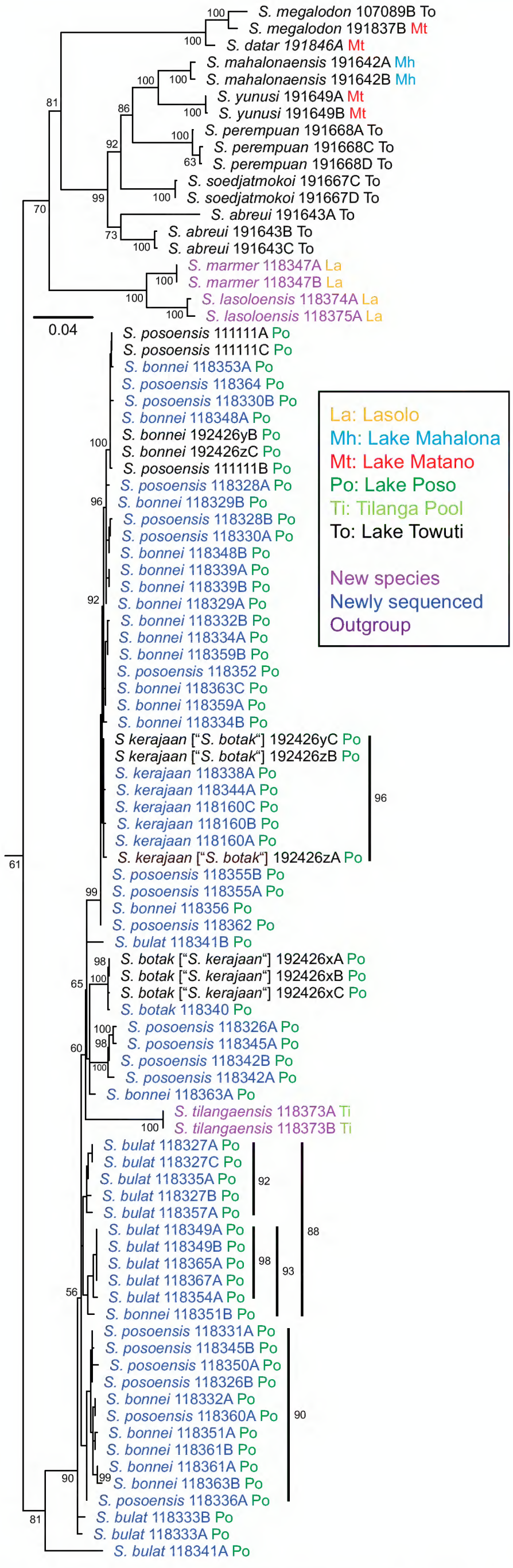
S. megalodon 107089B To
S. megalodon 191837B Mt
S. datar 191846A Mt
S. mahalonaensis 191642A Mh
S. mahalonaensis 191642B Mh
S. yunusi 191649A Mt
S. yunusi 191649B Mt
S. perempuan 191668A To
S. perempuan 191668C To
S. perempuan 191668D To
S. soedjatmokoi 191667C To
S. soedjatmokoi 191667D To
S. abreui 191643A To
S. abreui 191643B To
S. abreui 191643C To
S. marmer 118347A La
S. marmer 118347B La
S. lasoloensis 118374A La
S. lasoloensis 118375A La
0.04
S. posoensis 111111A Po
S. posoensis 111111C Po
S. bonnei 118353A Po
S. posoensis 118364 Po
S. posoensis 118330B Po
S. bonnei 118348A Po
S. bonnei 192426yB Po
S. bonnei 192426zC Po
S. posoensis 111111B Po
S. posoensis 118328A Po
S. bonnei 118329B Po
S. posoensis 118328B Po
S. posoensis 118330A Po
S. bonnei 118348B Po
S. bonnei 118339A Po
S. bonnei 118339B Po
S. bonnei 118329A Po
S. bonnei 118332B Po
S. bonnei 118334A Po
S. bonnei 118359B Po
S. posoensis 118352 Po
S. bonnei 118363C Po
S. bonnei 118359A Po
S. bonnei 118334B Po
S kerajaan ["S. botak"] 192426yC Po
S kerajaan ["S. botak"] 192426zB Po
S. kerajaan 118338A Po
S. kerajaan 118344A Po
S. kerajaan 118160C Po
S. kerajaan 118160B Po
S. kerajaan 118160A Po
S. kerajaan ["S. botak"] 192426zA Po
S. posoensis 118355B Po
S. posoensis 118355A Po
S. bonnei 118356 Po
S. posoensis 118362 Po
S. bulat 118341B Po
S. botak ["S. kerajaan"] 192426xA Po
S. botak ["S. kerajaan"] 192426xB Po
S. botak ["S. kerajaan"] 192426xC Po
S. botak 118340 Po
S. posoensis 118326A Po
S. posoensis 118345A Po
S. posoensis 118342B Po
S. posoensis 118342A Po
S. bonnei 118363A Po
S. tilangaensis 118373A Ti
S. tilangaensis 118373B Ti
S. bulat 118327A Po
S. bulat 118327C Po
S. bulat 118335A Po
S. bulat 118327B Po
S. bulat 118357A Po
S. bulat 118349A Po
S. bulat 118349B Po
S. bulat 118365A Po
S. bulat 118367A Po
S. bulat 118354A Po
S. bonnei 118351B Po
S. posoensis 118331A Po
S. posoensis 118345B Po
S. posoensis 118350A Po
S. posoensis 118326B Po
S. bonnei 118332A Po
S. posoensis 118360A Po
S. bonnei 118351A Po
S. bonnei 118361B Po
S. bonnei 118361A Po
S. bonnei 118363B Po
S. posoensis 118336A Po
S. bulat 118333B Po
S. bulat 118333A Po
S. bulat 118341A Po
La: Lasolo
Mh: Lake Mahalona
Mt: Lake Matano
Po: Lake Poso
Ti: Tilanga Pool
To: Lake Towuti
New species
Newly sequenced
Outgroup

Figure 11. Part of maximum likelihood tree including the new and newly sequenced species. Bootstrap values given if > 50 and provided graphical resolution due to short branch lengths permitting.

(Fig. 4C), teleoconch with growth lines, otherwise without structure; umbilicus a narrow slit, outer lip straight.

Remarks. Only five adult specimens could be morphologically examined. Therefore, i.e. because of the lack of anatomical data, the differentiation and diagnosis had to be restricted to genetic data. Phylogenetically, *S. tilangaensis* sp. nov. was nested among the species from Lake Poso with a long branch indicating considerable genetic differentiation (Figs 10, 11). Morphologically, the new species is similar to *S. bonnei* (see Haase and Bouchet 2006). As *S. bonnei* cannot be distinguished from *S. bulat* and *S. posoensis* based on mitochondrial data due to paraphyly (Zielske et al. 2011, see below), the new species was compared against those three species. *Sulawesidrobia tilangaensis* sp. nov. had diagnostic bases at 18 positions (type 1 *sensu* Kühn and Haase 2018) in the COI alignment (Suppl. material 1): position 50 (base C), 157 (T), 181 (G), 200 (A), 265 (G), 286 (G), 301 (G), 340 (T), 370 (G), 397 (C), 454 (G), 481 (G), 484 (G), 511 (G), 532 (C), 544 (G), 577 (G), 578 (C).

Morphometry

Shell variability within and among the new species is shown in the plot of the PCA in Fig. 10A. The first three principal components explained 93.97% of the total variance. Component 1 was dominated by number of whorls and shell height with small values on the left and large on the right side. Component 2 mainly described the variance of body-whorl width and shell width. Slender shells had small, largely negative values, stouter ones scored higher, mostly positively. The broader specimens of both samples of *S. lasoloensis* sp. nov. overlapped, but several specimens from the type locality were much more slender, hence scored lower along at least one of the axes.

In the discriminant analysis (Fig. 9B) with three significant axes, overlap was minimized, but the separation of both *S. lasoloensis* sp. nov. samples was still incomplete. An assignment test classified 97.78% of the shells correctly, i.e. only one specimen from the type locality of *S. lasoloensis* sp. nov. was allocated to the other sample of this species. A MANOVA was highly significant (Wilks' lambda = 0.0157, $DF_1 = 18$, $DF_2 = 102.3$, $F = 19$, $p < 0.0001$) and also all pairwise Hotelling's T^2 comparisons were significant after sequential Bonferroni correction.

Phylogenetic analysis

ML and BI gave largely identical tree topologies (Figs 10, 11, Suppl. material 2). Clade 1 with species from Lakes Matano and Towuti was sister to two clades, one again containing species from Lakes Mahalona, Matano and Towuti (Clade 2), and the other one comprising all species from Lake Poso (Clade 3). The new species from the SE, *S. lasoloensis* sp. nov. and *S. marmer* sp. nov., were part of Clade 2 and formed the sister group to all other species. The third new species, *S. tilangaensis* sp. nov., clustered with a long branch with the species from Lake Poso in Clade 3 (Figs 10, 11, Suppl. material 2). All other newly collected samples from Lake Poso were allocated to one of the following already described species: *S. bonnei*, *S. botak*, *S. bulat*, *S. kerajaan*, or *S. posoensis*. Of these, only *S. botak* and *S. kerajaan* were monophyletic. Most branches in this clade were short.

Discussion

With the three new species, we report for the first time tateid gastropods on Sulawesi outside of lakes. *Sulawesidrobia tilangaensis* sp. nov. occurs in a spring-fed pool in South Sulawesi, and *S. lasoloensis* sp. nov. and *S. marmer* sp. nov. were found in small streams in Southeast Sulawesi. The latter two species formed the sister clade to a clade containing species from the Malili lakes while *S. tilangaensis* sp. nov. was apparently closely related to species from Lake Poso. These relationships reflect geography to some degree, but the low number of non-lacustrine samples of *Sulawesidrobia* to date renders any discussion of biogeography rather speculative. A case in point is the close relationship of *S. tilangaensis* sp. nov to the Lake Poso species flock. Its type locality, Tilanga Natural Pool, also harbors an endemic species of ricefish, *Oryzias eversi* Herder, Hadiaty & Nolte, 2012, which is sister to a species endemic to Lake Lindu (Sutra et al. 2019) situated NW of Lake Poso in a completely different catchment. This strikingly different pattern can hardly be meaningfully discussed without a better overview of the distribution of *Sulawesidrobia*.

Considering the long branches as well as the geographic distances between the new species and their respective lake relatives as well as the large unexplored areas, many more species dwelling in similar, for tateids more typical (Ponder 2019) habitats are to be expected. We hope that our findings will stimulate further research into the diversity and distribution of this group of freshwater gastropods. This will be of relevance to the understanding of origin and evolution of *Sulawesidrobia* and allies, and – assuming similar distribution patterns characterized by a high degree of endemicity seen in other regions (e.g., Haase and Bouchet 1998; Haase 2008; Zielske and Haase 2014; Ponder et al. 2019) – for the freshwater biodiversity as well as conservation.

As in the analysis of Zielske et al. (2011), *S. bonnei* and *S. posoensis* were paraphyletic. Both species are widespread throughout the lake and fairly variable. We now found the same for *S. bulat*. Morphologically, populations assigned to these three species are fairly variable and we cannot exclude the existence of cryptic species. Based on formalin fixed material, Haase and Bouchet (2006) have described two species similar in shell shape to and sympatric with *S. bonnei* each at a single site. However, the entire clade is characterized by short branches. Clear and well supported subclades are exceptional and coincide with morphologically and anatomically well differentiated species only in the cases of *S. botak* and *S. kerajaan*, both with a limited range on the W-coast (Haase and Bouchet 2006; Fig. 1). This indicates that the entire radiation of *Sulawesidrobia* in Lake Poso is probably

young and incomplete lineage sorting and/or introgression are frequent, as has been suggested for the radiations of *Tylomelania* in the Sulawesi lakes (von Rintelen et al. 2012). This is in contrast to the relationships we observe in the Malili lake system, where species are genetically well differentiated with the exception of the paraphyly of *S. datar* Zielske, Glaubrecht & Haase, 2011 with respect to *S. megalodon* Zielske, Glaubrecht & Haase, 2011 (Zielske et al. 2011; Haase et al. 2023). This difference in pattern suggests different geological and/or ecological conditions over time providing the setting for speciation. Interestingly, the radiations of *Tylomelania* in Lake Poso and the Malili lakes do not show any differences in this respect between both lake systems, being equally poorly differentiated by mtDNA at the species level. The biological side of this question may be tackled using genomic data.

Acknowledgements

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Supplementary material 1

Alignment of *S. bonnei*, *S. bulat*, *S. posoensis*, and *S. tilangaensis* sp. nov. for molecular diagnosis of the latter

Authors: Laura Kadow, Thomas von Rintelen, Muhammad Iqram, Jean-Michel Bichain, Martin Haase

Data type: docx

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Link: https://doi.org/10.3897/zse.101.161812.suppl1

Supplementary material 2

50% majority rule consensus tree from Bayesian analysis. Posterior probabilities given provided graphical resolution due to short branch lengths permitting

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Data type: eps

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